

The succession of *Hyracotherium* (*Perissodactyla*, Mammalia) in the English early Eocene

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Synopsis

In the light of recently-collected material and the documentation of old stratigraphical information, the English species of *Hyracotherium* are re-evaluated with a better knowledge of variation and diagnostic characters. A phylogeny is suggested and some correlations within Europe are proposed.

Introduction

The morphology of British *Hyracotherium* has been exhaustively treated by previous authors (Owen 1841, 1842, 1858; Cooper, C. F. 1932*b*; Simpson 1952) but two types of data, one old and one new, put it in a different perspective and produce somewhat different taxonomic and evolutionary conclusions. These data are a good knowledge of the stratigraphic position of most of the specimens, which had not previously been fully appreciated, and an increase in the number of specimens known from the Blackheath Beds and the Suffolk Pebble Beds by recent collecting, giving a better idea of the degree of variation and more reliable dental characters. Since Simpson's (1952) revision of British material new specimens have been collected, mainly from Abbey Wood, by S. A. Baldwin, D. Bone, J. Collins, J. Cooper, A. Gale, W. H. George, P. R. Gurr, K. J. Hall, R. A. D. Markham, A. R. G. Packman, P. R. Payne, D. J. Ward, K. Wright and the author.

The registered numbers of specimens in the various institution collections are indicated by the following prefix letters: British Museum (Natural History), London (M or no prefix); Sedgwick Museum, Cambridge (C); Ipswich Museum, Suffolk (IM); Muséum National d'Histoire Naturelle, Paris (MU, AV or AL); University of California Museum of Paleontology, Berkeley (UC).

Symbols used in synonymies as in Matthews (1973).

Stratigraphy

Simpson (1952 : 202), referring to the holotypes of *H. leporinum* and *H. vulpiceps*, stated: 'their relative levels within the London Clay have not been, and perhaps cannot be, established'. The horizon of the latter is recorded by Owen (1858 : 55) as the Roman Cement bed at Harwich (= Harwich cement stone (Davis & Elliott 1951 : 331) and the Harwich Stone Band (Elliott 1971)) which occurs 6 m above the base of the London Clay. This is now known to be an important ash marker (Elliott 1971) and is correlated with a Greenland volcanic episode dated at 53 Ma (Fitch *et al.* 1978). The lithology of the adherent matrix shows the quoted provenance to be correct. The age-equivalent deposit in Denmark, the Mo Clay, belongs to the calcareous nannoplankton zone 10.

The horizon of the holotype of *H. leporinum* is less accurately known but details of its collection from the cliff at Studd Hill, near Herne Bay, were given by Richardson (1841). Remains of the crinoid *Isselocrinus subbasaltiformis* (Miller) were formerly to be found (Cooper, J. 1977 : 173; Gamble 1979) about half-way up the cliff before the section was obscured by sea defences. This species has a restricted range in the London Clay between about 27 m and 37 m above the base (= Division 2 of Wrigley, 1924; King 1970). Its main occurrence at Studd Hill is restricted to 31–32 m above the base (Gamble 1979). The holotype of *Hyracotherium leporinum* evidently came from the vicinity of this horizon and thus occurs significantly higher than the holotype of *H.*

vulpiceps. A second specimen of *H. leporinum* from the Herne Bay foreshore (C. B. Brown collection), now in the Sedgwick Museum, Cambridge, is most likely to be from the same horizon.

An imperfect cranium of *H. vulpiceps* (38801) is not, as quoted by Cooper, C. F. (1932b : 433) and Simpson (1952 : 195), from Sheppey but, according to the British Museum (Natural History) Palaeontology Department register, 'from the Crag (wreck of London Clay)'; i.e. from the Red Crag basement bed of Suffolk. This is of late Pliocene age but contains much material derived from the London Clay. The dark reddish, highly polished surface of the adherent matrix shows the quoted provenance to be correct. The original horizon in the London Clay is, of course, unknown but today only the lower part is preserved in Suffolk below the unconformity at the base of the Red Crag.

Further British specimens that have been attributed to *Hyracotherium* are two mandibular fragments without tooth crowns (38939, 47986; see Lydekker 1886 : 11) from the London Clay of Sheppey. They are generically indeterminable but the horizontal ramus (38939) is very similar to that of the holotype of *H. vulpiceps* in size and morphology. Further specimens would be very interesting in view of the later Cuisian age indicated by Costa & Downie (1976 : 600, 603) for this part of the succession.

Specimens, here identified as *H. aff. vulpiceps*, from Abbey Wood, occur in the Abbey Wood member of the Blackheath Beds which underlie the London Clay. The associated fauna is as follows:

- Charlesmooria childei* Kühne, 1969
- ? *Didelphodus* sp.
- Didelphodontinae indet.
- ? *Eochiromys* sp.
- ? *Macrocranion* sp.
- Adapisoricidae indet.
- '*Adapisorex*' *anglicus* C. F. Cooper, 1932a
- Phenacolemur* cf. *fuscus* Russell, Louis & Savage, 1967
- Teilhardina* sp.
- Pelycodus eppsi* (C. F. Cooper, 1932a)
- Esthonyx* sp.
- Microparamys* sp.
- Paramyidae indet.
- ? *Prototomus* sp.
- Oxyaena* sp.
- Arctocyonidae indet.
- Hyopsodus wardi* Hooker, 1979
- Lessnessina packmani* Hooker, 1979
- ? *Phenacodus* sp.
- Coryphodon eocaenus* Owen, 1846
- Hyracotherium* aff. *vulpiceps* (Owen, 1858)
- Protodichobune* sp. 1

The specimens of *H. cuniculus* from Kyson came from the Suffolk Pebble Beds, which immediately underlie the London Clay in Suffolk, and further specimens are here recorded for the first time from the same beds at Bramford and Ferry Cliff. The Suffolk Pebble Beds have often been synonymized or equated in age with the Blackheath or Oldhaven Beds because of their identical position below the London Clay and their superficial lithological similarity. However, their mammal fauna is different from that of Abbey Wood, its overall aspect being more primitive and rather similar to those of Dormaal and Erquelinnes, Belgium (Quinet 1969; Gingerich 1976 : text-fig. 18). The fauna is as follows (locality initials indicated for Bramford, Ferry Cliff, Harwich and Kyson):

- | | |
|---|-------|
| Leptictidae indet. | K, FC |
| <i>Paschatherium dolloi</i> (Teilhard de Chardin, 1927) | FC |

| | |
|---|----------|
| <i>Plesiadapis</i> aff. <i>remensis</i> Lemoine, 1887 | K |
| <i>P.</i> aff. <i>tricuspidens</i> Gervais, 1877 | FC |
| Omomyidae indet. | FC |
| <i>Pelycodus</i> sp. | K |
| <i>Paramys</i> sp. | K, FC |
| <i>Meldimys</i> sp. | FC, ? i |
| ? <i>Prototomus</i> sp. | K |
| Creodonta indet. | K |
| Miacidae indet. | K |
| <i>Landenodon</i> sp. | K, FC, H |
| <i>Microhyus musculus</i> Teilhard de Chardin, 1927 | K, FC, H |
| <i>Hyopsodus</i> cf. <i>wardi</i> Hooker, 1979 | K |
| ? <i>Coryphodon</i> sp. | FC |
| <i>Hyracotherium cuniculus</i> Owen, 1842 | K, FC, B |
| <i>Protodichobune</i> sp. 2 | K |

Boswell (1916 : 571) stated: 'the lithology and petrology of the pebble bed suggests that it should be grouped with the Reading Beds, but its fauna is a typical London Clay assemblage'; but also (1916 : 566) 'unfortunately the species [molluscs and fish] are of rather wide range, and are not sufficient to form the basis of any correlation'. The Suffolk Pebble Beds (White 1931 : 40) are here accepted as distinct from the Blackheath or Oldhaven Beds, and somewhat older. The stratigraphical evidence for the English *Hyracotherium* succession is shown in the geological columns in Fig. 6, p. 111.

Morphology

Most authors have agreed on the separation of at least two English *Hyracotherium* species on the basis of size (smaller *H. cuniculus* and larger *H. leporinum* and *vulpiceps*), but opinions on the validity of the separation of the two larger ones have varied (see synonymy lists). Simpson (1952 : 202) found the teeth to vary so much that 'no other specimens show exactly the same distinction as these types [the holotypes of *H. leporinum* and *H. vulpiceps*] and none can be referred with real clarity to one species rather than the other'. In the stratigraphically-controlled assemblages mentioned above certain characters do in fact show a distinctness which can be used for specific separation. On the other hand, additional specimens from Abbey Wood strengthen Simpson's (1952 : 202) view of the variability of other characters such as the lingual cingulum. The characters found to be of low variability and useful in separating species and recognizing trends are as follows:

1. Configuration of upper molar centrocrista (and to a certain extent the presence of a meso-style)
2. Structure and size of M_3 hypoconulid lobe
3. Shape and structure of P^3
4. Overall size of teeth.

Features of the skull discussed in detail by Simpson (1952 : 196-200) and Savage *et al.* (1965 : 49-50) are not considered here because they are known for only two specimens (one each of *H. leporinum* and *H. vulpiceps*) and their variability cannot be assessed.

Systematic descriptions

Family EQUIDAE Gray, 1821

Genus *HYRACOTHERIUM* Owen, 1841

- 1841 *Hyracotherium* Owen : 203-208.
 1846 *Macacus* Desmarest; Owen : 1-10.
 1858 *Pliolophus* Owen : 54-71; pls 2-4.
 1876 *Eohippus* Marsh : 401.

1880 *Lophiodochoerus* Lemoine : 589 (*vide* Teilhard de Chardin 1922 : 67).

1896 *Protorohippus* Wortman : 92, figs 14–15.

TYPE SPECIES. *Hyracotherium leporinum* Owen, 1841.

REMARKS. The most recent generic diagnosis (Kitts, 1956) is evidently unsatisfactory as the type species tends to have a weak upper molar mesostyle and *H. vulpiceps* either has no P_1^1 – P_2^2 diastema or this feature is intraspecifically variable. A revised diagnosis should await a full revision of the North American species.

Hyracotherium cuniculus Owen, 1842

Fig. 1a–c

- v 1839 *Macacus*; Wood : 444–445, text-fig. 57.
- v 1839 *Macacidae*; Owen : 446–448, text-fig. 58.
- v* 1842 *Hyracotherium Cuniculus* Owen : 1–2, text-figs 2, 5.
- v 1846 *Macacus eocaenus* Owen : 1–10, text-figs 1, 3.
- v 1927 *Hyracotherium* sp.; Teilhard de Chardin : 27–28, text-fig. 28c; pl. 5, fig. 22.
- v 1932b *Hyracotherium cuniculus* Owen; C. F. Cooper : 438–441, text-figs 1A, C, 2B, E, F; pl. 51, figs 6–9.
- v 1952 *Hyracotherium cuniculus* Owen; Simpson : 196–204, text-fig. 4B.

TYPES. The left M^3 , 36569 (Owen 1842 : text-fig. 2, reversed) was chosen as lectotype by Simpson (1952 : 196). One of the figured paralectotypes, the right $M^{1/2}$ M29709 (re-registered from 36569; Owen 1842 : text-fig. 5, reversed), is correctly identified. The distal half of a left $M^{1/2}$ M14111 (re-registered from 36572) may be Owen's unfigured paralectotype. Owen's supposed upper premolar (1842 : text-fig. 4, third paralectotype) looks most like M29699, which is a right M^2 of *Landenodon*.

OTHER MATERIAL. This is listed in the table of measurements, Table 1.

TYPE HORIZON AND LOCALITY. Suffolk Pebble Beds of Kyson, near Woodbridge, Suffolk (Nat. Grid TM 270475; see Prestwich 1850 : 272–273).

RANGE. Suffolk Pebble Beds of Bramford (TM 130477; Cooper, J. 1976) and Ferry Cliff near Woodbridge (TM 278486; George & Vincent 1976 : 25), both Suffolk. Also the Sables d'Erquelines of Erquelines (=Jeumont), Hainaut, Belgium (Rutot 1881).

EMENDED DIAGNOSIS. Small species of *Hyracotherium* (see Table 1), length of P^2 – M^3 estimated 35 mm. Upper molars with straight centrocrista and no trace of a mesostyle. Lower molar metalophids tend to join trigonids nearer to protoconids than to metaconids. M_3 hypoconulid lobe small, tending to be buccal in position. P^3 with small protoconule; centrolingually placed protocone; straight mesiolingual margin; no postprotocrista.

DISCUSSION. Five individuals with lower molars and specifically four M_3 s, four upper molars and two P^3 s are available from the Suffolk Pebble Beds to demonstrate the constancy of the diagnostic characters. The right M_3 figured by Teilhard de Chardin (1927 : pl. 5, fig. 22) from Erquelines fits *H. cuniculus* in size and morphology as this author noted. According to Quinet & Verlinden's (1970) measurements, the Erquelines mandible figured first by Rutot (1881) is too big for *H. cuniculus*, being about the size of *H. vulpiceps*, but the metalophid joins the trigonid just buccal to the midpoint, more like *H. cuniculus* than *H. vulpiceps*. The small diastema between P_1 and P_2 is probably of little taxonomic value.

Hyracotherium vulpiceps (Owen, 1858)

Fig. 3a–c

- v* 1858 *Pliolophus vulpiceps* Owen : 54–71; pls 2–4.
- v 1865 *Hyracotherium leporinum* Owen; Owen : 340; pl. 10, fig. 2.
- v 1886 *Hyracotherium leporinum* Owen; Lydekker : 11.

Table 1. Maximum length (l) and width (w) measurements (mm to the nearest 0.1) of English *Hyracotherium*. The following localities are indicated by their initials: Bramford, Ferry Cliff, Kyson, Abbey Wood, Harwich, Herne Bay, Suffolk (Red Crag basement bed). L = left, R = right.

Hyracotherium cuniculus

| Number | Locality | tooth | l | w | Number | Locality | tooth | l | w |
|-------------|----------|-------------------|-------|-------|---------------|----------|---------------------|-------|-----|
| M14112 | K | LP ³ | (4.4) | 5.2 | M29701 | K | LM _{1/2} | — | 3.9 |
| 36572 | K | LP ³ | 5.1 | 5.6 | M36494 | FC | RM ₂ | 7.3 | 5.1 |
| M29709 | K | RM ^{1/2} | (6.3) | 8.1 | | | RM ₃ | (8.8) | 4.6 |
| M14111 | K | LM ^{1/2} | — | (6.4) | M36495 | FC | RM _{1/2/3} | — | 5.0 |
| M36496 | FC | LM ^{1/2} | 6.6 | — | M29710 | K | RM ₃ | 8.7 | 4.7 |
| IM 1971-169 | B | LM ^{1/2} | 7.5 | — | M14113 | K | RM ₃ | 8.5 | 4.9 |
| 36569 | K | LM ³ | 6.4 | 7.6 | IM 1951-28-25 | K | RM ₃ | 8.4 | 4.8 |

Hyracotherium aff. *vulpiceps*

| | | | | | | | | | |
|-----------------|-----|---------------------|-----------------|-------|-----------|----|-------------------|------|-----------------|
| M13761 | AW | RP ³ | 6.0 | 6.8 | M29646 | AW | LDP ³ | 5.4 | — |
| | | RP ¹ | 6.7 | 8.1 | M13763-4 | AW | RDP ₁ | 6.9 | 4.5 |
| | | RM ¹ | 7.6 | 9.2 | | | RM ₁ | 7.2 | 5.3 |
| RM ² | 8.3 | 10.0 | RM ₂ | 7.9 | | | 6.0 | | |
| M26564 | AW | LDP ¹ | 7.1 | 8.1 | M29719-21 | AW | RM ₁ | 7.2 | 5.1 |
| | | LM ¹ | 7.7 | 9.2 | | | RM ₂ | 8.3 | 5.6 |
| M25129 | AW | LDP ¹ | 6.6 | 8.1 | | | RM ₃ | 9.8 | 5.1 |
| M32142 | AW | LM ¹ | 7.5 | 8.9 | M26906 | AW | RM ₂ | 7.6 | 5.3 |
| | | LP ¹ | 6.3 | 8.0 | | | RM ₃ | 10.5 | 5.5 |
| M29716 | AW | RM ^{1/2} | 7.7 | (8.8) | | | M29360 | AW | RP ₃ |
| M29754 | AW | RM ^{1/2} | 7.2 | 8.7 | M29715 | AW | LP ₁ | 5.9 | 4.3 |
| M15140a | AW | RM ^{1/2} | 7.6 | — | M32127 | AW | RM _{1/2} | 8.0 | 5.6 |
| M15139 | AW | LM ³ | 7.8 | 9.8 | M15143 | AW | RM _{1/2} | 8.2 | 5.6 |
| M13762 | AW | LM ³ | 7.9 | 9.2 | M29744 | AW | LM ₃ | 10.3 | 5.4 |
| M15138 | AW | LM ³ | 8.4 | (8.8) | M15130 | AW | RM ₃ | 10.6 | 5.5 |
| M15140b | AW | RM ^{1/2/3} | — | — | M13765 | AW | RDP ₃ | — | 3.6 |
| M29231 | AW | LDP ³ | 6.8 | 6.2 | M29645 | AW | RDP ₄ | 7.3 | 4.6 |

Hyracotherium vulpiceps

| | | | | | | | | | |
|-------|---|-----------------|-------|-------|-----------------|--------|-----------------|-------|-------|
| 44115 | H | RP ¹ | — | — | 44115 | H | RP ₁ | (3.8) | (2.2) |
| | | RP ² | 5.6 | 4.3 | | | RP ₂ | (6.0) | (2.7) |
| | | RP ³ | 6.1 | 6.6 | | | RP ₃ | (6.3) | (3.8) |
| | | RP ⁴ | 6.6 | 7.9 | | | LP ₄ | 6.6 | 4.6 |
| | | RM ¹ | 7.2 | 9.0 | | | LM ₁ | 7.4 | 5.5 |
| | | RM ² | 8.9 | 10.1 | | | LM ₂ | 8.5 | (6.0) |
| 38801 | S | LM ³ | 7.5 | 8.9 | RM ₃ | (10.5) | 6.1 | | |
| | | LP ² | (6.5) | (3.5) | | | | | |
| | | RP ³ | 6.4 | 6.7 | | | | | |
| | | RP ⁴ | 7.2 | 8.3 | | | | | |
| | | RM ¹ | 7.6 | 9.5 | | | | | |
| | | RM ² | 8.2 | 10.2 | | | | | |
| | | RM ³ | 7.6 | 9.5 | | | | | |

Hyracotherium leporinum

| | | | | | | | | | |
|--------|----|-----------------|-----|------|--------|----|-----------------|-----|------|
| M16336 | HB | RP ² | 5.9 | 3.5 | C21361 | HB | RP ² | 6.9 | 4.1 |
| | | LP ³ | 6.8 | 7.3 | | | LP ³ | 6.7 | 7.0 |
| | | LP ⁴ | 6.9 | 8.5 | | | LP ⁴ | 7.6 | 8.8 |
| | | RM ¹ | 7.7 | 9.7 | | | LM ¹ | 8.0 | 10.3 |
| | | RM ² | 8.6 | 10.5 | | | LM ² | 8.5 | 11.0 |
| | | RM ³ | 8.5 | 10.0 | | | RM ³ | 8.1 | 10.4 |

- v 1901 *Hyracotherium leporinum* Owen; Depéret : 200–201; pl. 4, fig. 1.
 v 1932b *Hyracotherium vulpiceps* (Owen); C. F. Cooper : 432–436, text-figs 2D, 3A; pl. 50, figs 1–3; pl. 51, figs 1–3.
 v 1952 *Hyracotherium vulpiceps* (Owen), Simpson : 195–206; pl. 37; pl. 38, figs a–d.
 v 1952 *Hyracotherium* sp.; Simpson : pl. 40, fig. a.

HOLOTYPE. The skull and incomplete skeleton 44115 (also registered on 44115a and M10657–61) still partly embedded in matrix. Simpson (1952 : 196) has described the history of this specimen. A subsequent misfortune has been the disappearance of the almost complete right mandibular ramus which appears to have happened about 1960.

OTHER MATERIAL. Damaged cranium with left P³–M² and right P³–M³, 38801.

TYPE HORIZON AND LOCALITY. The Harwich Stone Band (= Roman cement bed), lower London Clay of Harwich, Essex.

RANGE. 38801 is from the Red Crag basement bed, assumed derived from the London Clay.

EMENDED DIAGNOSIS. Medium-sized species of *Hyracotherium* (see Table 1), length of P²–M³ 41 mm in holotype. Upper molars with very slightly buccally flexed centrocrista and a very faint rib in the mesostylar position, separated from the buccal cingulum. Lower molar metalophids tend to join trigonids equidistant between protoconids and metaconids. M₃ hypoconulid lobe relatively large and with a median main cusp. P³ with large protoconule; distolingually placed protocone; slightly convex mesiolingual margin and little or no postprotocrista.

DOUBTFULLY REFERRED SPECIMENS. There are four other specimens the size of *H. vulpiceps* in the Ipswich Museum from the Red Crag basement bed, presumed to be derived from the London Clay. A palate (IM 1935-64a; E. C. Moor collection) with all the cheek tooth crowns broken off has a P³ with typical *vulpiceps* outline but, unlike the holotype, a short diastema between P¹ and P². A P¹–P² diastema was used as a generic character by Kitts (1956). A right maxillary fragment with P⁴–M² (IM 1935-64b) has upper molar centrocrista with buccal flexure intermediate between the condition in *H. vulpiceps* and that in *H. leporinum*, and P⁴ with a slight distal protoconal crest trending distobuccally. A right mandibular fragment with M_{2–3} (IM 1935-64c) has a typically long M₃ hypoconulid lobe. The fourth specimen (IM unnumbered, old collection) is from Falkenham, Suffolk, and is a palate with apparently left and right DP³–M² very abraded. The last two specimens could, on the basis of size, be referred to either *H. vulpiceps* or *H. leporinum*.

Hyracotherium aff. *vulpiceps*

Fig. 2a–c

- v 1931 *Hyracotherium* sp.; White : 18, 25.
 v 1932b *Hyracotherium vulpiceps* (Owen); C. F. Cooper : 433, 437–438; pl. 51, figs 4–5.
 v 1952 *Hyracotherium* sp.; Simpson : pl. 40, figs b–d.

MATERIAL. See Table 1.

RANGE. Abbey Wood member of the Blackheath Beds, Abbey Wood, London Borough of Bexley (TQ 4801 7864). Also possibly the Blackheath Beds of Bean, Kent (TQ 590717) based on an upper molar hypoconal fragment (M32179, J. Cooper collection).

DISCUSSION. The Abbey Wood specimens show a very close resemblance to the holotype of *H. vulpiceps* in size and morphology, with the exception of the unique P³ (M13761). This differs in having a small protoconule, centrolingually placed protocone and straight mesiolingual margin. It thus resembles P³ of *H. cuniculus* in morphology, but is larger. The combination of very small numbers and different morphology of P³ in the *H. vulpiceps*/aff. *vulpiceps* complex can be treated in two different ways. We may combine them into one species on the basis of molar identity and

assume that the P³s are variable, or we can consider the two assemblages as different on a typological basis, but closely related. The second approach is here preferred as it is less subjective and in particular because the P³ of *H. cuniculus* and of *H. leporinum* are distinct, contrary to Simpson's statement (1952 : 203).

The constancy of molar characters in *H. vulpiceps* and *H. aff. vulpiceps* is supported by the upper molars of eleven individuals, the lower molars of eight individuals and specifically the M₃s of five individuals. The left M³ (M13762, figured C. F. Cooper 1932b : pl. 51, fig. 4 lower) shows a straight centrocrista probably as a result of the tapering of the end of the tooth row, which has also resulted in a very lingual metacone.

Hyracotherium leporinum Owen, 1841

Fig. 4a–b

- v* 1841 *Hyracotherium leporinum* Owen : 203–208; pl. 2, figs 1–4.
- v 1846 *Hyracotherium leporinum* Owen; Owen : 419–423, text-figs 165–167.
- v 1932b *Hyracotherium leporinum* Owen; C. F. Cooper : 431–446, text-fig. 3B; pl. 49; pl. 50, fig. 4.
- v 1952 *Hyracotherium leporinum* Owen; Simpson : 195–206; pl. 39, fig. a.
- v 1952 *Hyracotherium* sp.; Simpson : pl. 39, fig. b.

HOLOTYPE. Facial part of cranium with alveoli or roots of both canines, both P¹s, left P^{2–3}, left M³ and crowns of right P^{2–M}³ and left P^{4–M}² (M16336).

OTHER MATERIAL. Palate with left and right P^{2–M}³ (C21361).

TYPE HORIZON AND LOCALITY. Approximately Division 2 of the London Clay; Studd Hill near Herne Bay, Kent (TR 153677). C21361, labelled 'foreshore Herne Bay', is probably also from here.

EMENDED DIAGNOSIS. Medium-sized species of *Hyracotherium* (see Table 1), length of P^{2–M}³ 43 mm in holotype. The two available specimens have slightly larger upper premolars and slightly wider upper molars than *H. vulpiceps* (see Fig. 5c–d). Upper molars with strongly buccally flexed centrocrista and weak mesostyle. (Lower molars unknown.) P³ with small protoconule; centrolingually placed protocone; slightly concave mesiolingual margin; strong postprotocrista present.

DISCUSSION. Of the diagnostic characters only the degree of development of the mesostyle is seen to be slightly variable between the two known upper dentitions; in C21361 it joins the buccal cingulum. In particular the degree of buccal flexing of the centrocrista does not vary and is distinct from *H. vulpiceps* and *H. cuniculus*. The fact that P³ has a postprotocrista and a slightly concave mesiolingual margin differentiates it from *H. cuniculus* (and from *H. vulpiceps*). Simpson's (1952 : 203) statement that they are very similar is incorrect and his text-fig. 4 is inaccurate. Detail of the postprotocrista in the two specimens is different, it being single and sharp in C21361 and a double structure in the holotype. In the holotype, P³ and P⁴ have a distal protoconal crest (? = postprotocingulum) which fades before reaching the distal cingulum; it is missing on C21361.

Evolutionary trends

Knowing the stratigraphical occurrences of most of the English specimens of *Hyracotherium*, one can see a progression of morphologies through time which shows evolutionary trends, if not the evolution of a single lineage. Figs 1–4 show the changes in P³, M^{1/2} and M₃ in four stages. There is a size increase from stage 1 to 2 and from stage 3a to 4a (the slight width increase of the upper molar from stages 3 to 4 is demonstrated in Fig. 5d, p. 109); the upper molar morphology remains the same from stage 2 to 3; the M₃ hypoconulid lobe enlarges, lengthens and becomes more median in position from stage 1 to 2 (and remains unchanged from 2 to 3). At the same time the attachment of the metalophid to the trigonid shifts lingually to a more median position. The actual lengthening of the hypoconulid lobe is demonstrated in Fig. 5a by measuring distances between cusp tips. *H. aff. vulpiceps* also shows a relative lengthening of the whole M₃ over *H. cuniculus* (Fig. 5b). The specimen of *H. aff. vulpiceps* which overlaps greatly with *H. cuniculus*

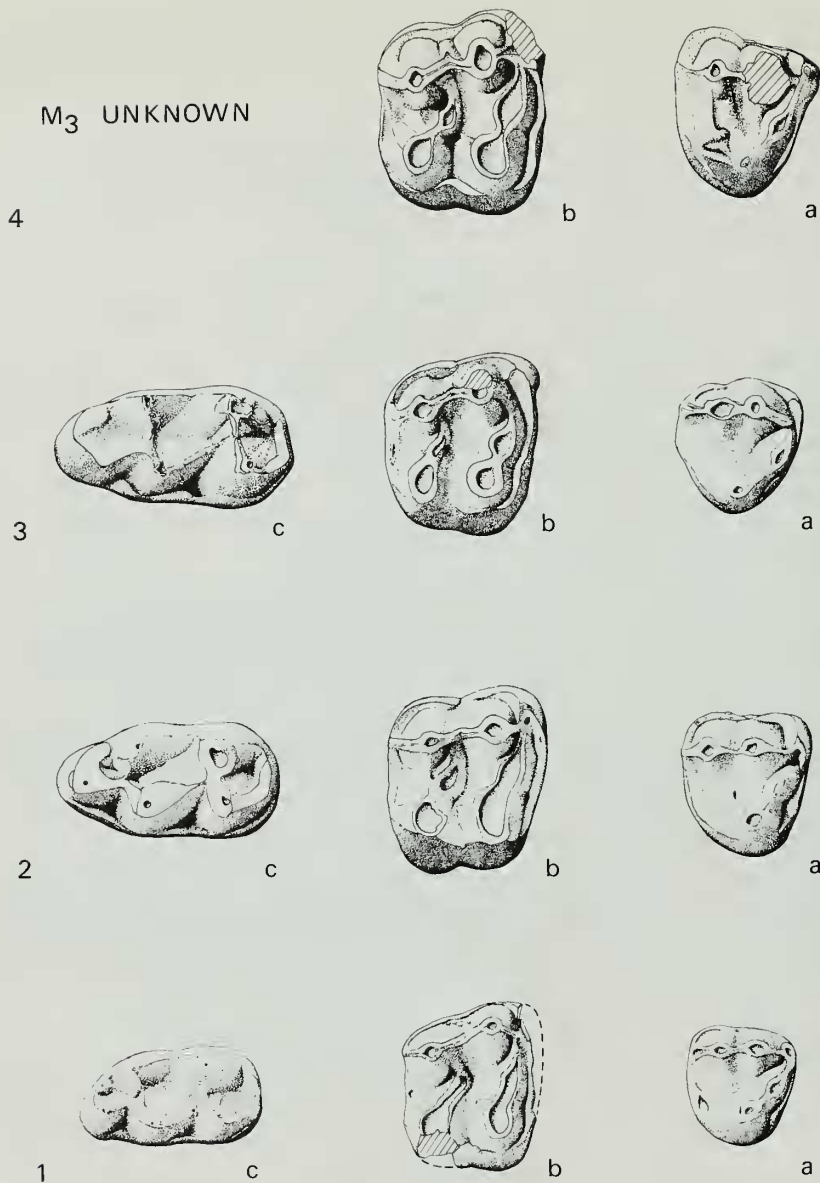


Fig. 1 *Hyracotherium cuniculus*, from the Suffolk Pebble Beds of Kyson, Suffolk: (a) left P³ (reversed) (36572); (b) right M^{1/2} (M29709); (c) right M₃ (M29710). All $\times 3$.

Fig. 2 *H. aff. vulpiceps*, from the Blackheath Beds of Abbey Wood, London: (a) right P³ (M13761); (b) left M¹ (reversed) (M25129); (c) right M₃ (M26906). All $\times 3$.

Fig. 3 *H. vulpiceps*, from the Harwich Stone Band, London Clay, Harwich, Essex; holotype (44115): (a) right P³; (b) composite left and right M¹ (shown as right); (c) right M₃ (drawn from photograph in Cooper, C. F. 1932b: pl. 51, fig. 1). All $\times 3$.

Fig. 4 *H. leporinum*, from approximately Division 2, London Clay, Herne Bay, Kent; holotype M16336: (a) right P³; (b) right M¹. All $\times 3$.

in hypoconulid length (M15130) is nevertheless typical in its overall length/width proportions and appears to have achieved this by relative elongation of the talonid.

Other variable characters such as angular development and outline shape of upper molars as well as different wear stages (specimens figured chosen as far as possible to show similar wear) make the specimens shown in Figs 1–4 appear more different from one another than their specific diagnoses indicate.

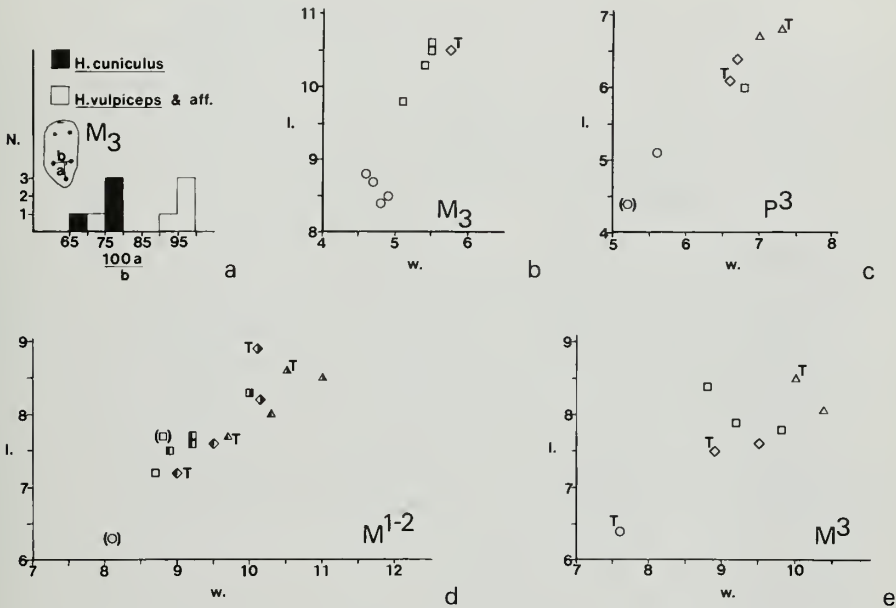


Fig. 5 (a) Histogram of perpendicular distance from hypolophid to hypoconulid (a), as a percentage of hypolophid length (b), in M_3 of *Hyracotherium cuniculus*, *H. vulpiceps* and *H. aff. vulpiceps*; (b–e) Scatter diagrams of maximum length (l) and width (w), in mm, of M_3 , P^3 , M^{1-2} and M^3 respectively. Symbols: *H. cuniculus* (○), *H. aff. vulpiceps* (□), *H. vulpiceps* (◇) and *H. leporinum* (△). Symbols in brackets indicate estimates; T indicates a plot of the primary type of a species; in Fig. 5d pre-ultimate molars identified as M^1 or M^2 are indicated by solid left or right half symbol, respectively.

C. F. Cooper (1932b : 442–443), unaware that *H. leporinum* occurred above *H. vulpiceps*, considered the latter to be more advanced because its P^3 resembled that of North American late Wasatchian forms such as *H. venticulum* (Cope), which were molarizing their premolars in the direction of *Orohippus*. In England, and probably the rest of Europe, the initial trend of molarization of P^3 by the North American equid method (i.e. by enlargement of the protoconule and distal shift of the protocone) changed to the European palaeothere method (i.e. by addition of a hypocone behind the protocone, as occurred in the molarization of P^1 in both North American and European equids) in the evolution of *Hyracotherium vulpiceps* to *H. leporinum*. It is possible that it was at this time that the Ypresian transgression finally isolated the North American and European Eocene mammal faunas, whereupon the palaeothere and equid characteristics established themselves.

Potential complications to the evolutionary scheme envisaged here are the *vulpiceps*-sized mandible occurring alongside the M_3 of *H. cuniculus* at Erquelines, and a poorly preserved palate (1M, unnumbered), with no data but in preservation identical to those from the Red Crag basement bed, the size of *H. cuniculus*. Nevertheless, the English sequence of species is a useful standard which might be recognized elsewhere in Europe and be used in biostratigraphic correlation. At the moment, however, the limits of the stratigraphical ranges of the various

species are too poorly known to erect legitimate biozones for them. Some correlations, however, are suggested below. The occurrences of *H. cuniculus* in the London and Belgian Basins probably mark the time of the initial migration into Europe of the Sparnacian mammal fauna. *Hyracotherium* species from the French Sparnacian, especially the higher parts, are not so easily comparable with the English species, and it is possible that the transgression of the Ypresian sea had by this time isolated the two areas, allowing evolution to occur independently.

Foreign specimens attributed to English species

Savage *et al.* (1965) described *Hyracotherium* from three Paris Basin Sparnacian sites (Pourcy, Mutigny and Avenay). At each the size variation for the few isolated teeth known exceeds that for the English species. In fact the measurements span those of *H. cuniculus* and either *H. vulpiceps* or *H. leporinum*. This fact was recorded by Savage *et al.* (1965) only for the Avenay locality and is reflected in their 'cf. *cuniculum*' (*sic*) identification of the smaller species there. In morphology all these French specimens differ from both *H. cuniculus* and *H. vulpiceps* in the frequent, but not constant, presence of buccally flexed centrocristae and development of mesostyles on the upper molars. Their figures of the upper molars from Pourcy (1965 : text-fig. 3b-d) show slight buccal flexing of the centrocrista. The smaller $M^{1/2}$ (1965 : text-fig. 3b) appears to have a fairly strong mesostyle whilst the larger M^3 s (1965 : text-figs 3c-d) appear to have a weaker one somewhat like *H. vulpiceps*. The two M^3 s from Mutigny (1965 : text-figs 2f, 2i) appear to have little flexure of the centrocristae and little or no sign of a mesostyle. However, another M^3 (MU12371) and an original (MU12329) and a cast (MU L-218) of two $M^{1/2}$ s, which I was able to see when in the Muséum National d'Histoire Naturelle, Paris, have the same centrocrystal flexure as *H. leporinum* and a slightly greater mesostyle development. The smaller type from Avenay (referred to by Savage *et al.* (1965 : 11) as *H. cf. cuniculum*) differs morphologically from *H. cuniculus*. The $M^{1/2}$ AV4790 (1965 : text-fig. 4c) has a strongly buccally flexed centrocrista and has a mesostyle, the P^4 (1965 : text-fig. 4b) has a weak fold on the distal protocone wall, like the holotype of *H. leporinum*, and the P^3 (1965 : text-fig. 4a) appears to have a well-developed postprotoconulum. The $M^{1/2}$ of the larger type from Avenay (1965 : text-fig. 4f) appears to have a weak centrocrystal flexure and no mesostyle. All the M_3 s from these three French Sparnacian sites have a relatively long hypoconulid lobe as in *H. vulpiceps* and unlike *H. cuniculus*.

AL5198, the left mandibular fragment with P_4 - M_3 from Lemoine's Agean fauna (a mixture from both the type Sparnacian and the younger Sables à Unios et Térédines), was originally described by Teilhard de Chardin (1922 : 70, text-fig. 33C; pl. 3, fig. 30) as *Propachynolophus* sp. nov. or sp. ind. Savage *et al.* (1965 : 13, text-fig. 4h) referred it to *Hyracotherium* and suggested that it was older than *Propachynolophus* (i.e. Sparnacian) and morphologically intermediate between the two. Its short hypoconulid lobe is reminiscent of *H. cuniculus* but there is no lingual accessory cusp and the animal was closer to *H. vulpiceps* in size. The apparently primitive M_3 suggests that this specimen might be from earlier in the Sparnacian than those from Pourcy, Mutigny and Avenay and it is possible that affinities might lie with the *vulpiceps*-sized mandible from Erquelinnes.

Teilhard de Chardin's (1922 : 52) fig. 26 indicates three teeth of a *Hyracotherium* the size of *H. cuniculus* from the Conglomérat de Meudon, near Paris (at base of the Argile Plastique, considered Sparnacian in age). His discussion, however, indicates an animal the size of *H. leporinum* and the M_3 hypoconulid lobe is indeed longer than that of *H. cuniculus*.

Correlation with continental Europe

Unfortunately, the Paris Basin *Hyracotherium* material is still too poorly known to identify specifically, but the specimens from Mutigny and Avenay appear to be as advanced as the stratigraphically highest English species (*H. leporinum*). This conforms with Gingerich's (1977 : fig. 8) proposed succession of Sparnacian localities based on the phylogeny of adapid primates. It also suggests, however, that the French Sparnacian localities Mutigny and Avenay are equivalent to the early Ypresian of England. Erquelinnes can be correlated with the Suffolk Pebble

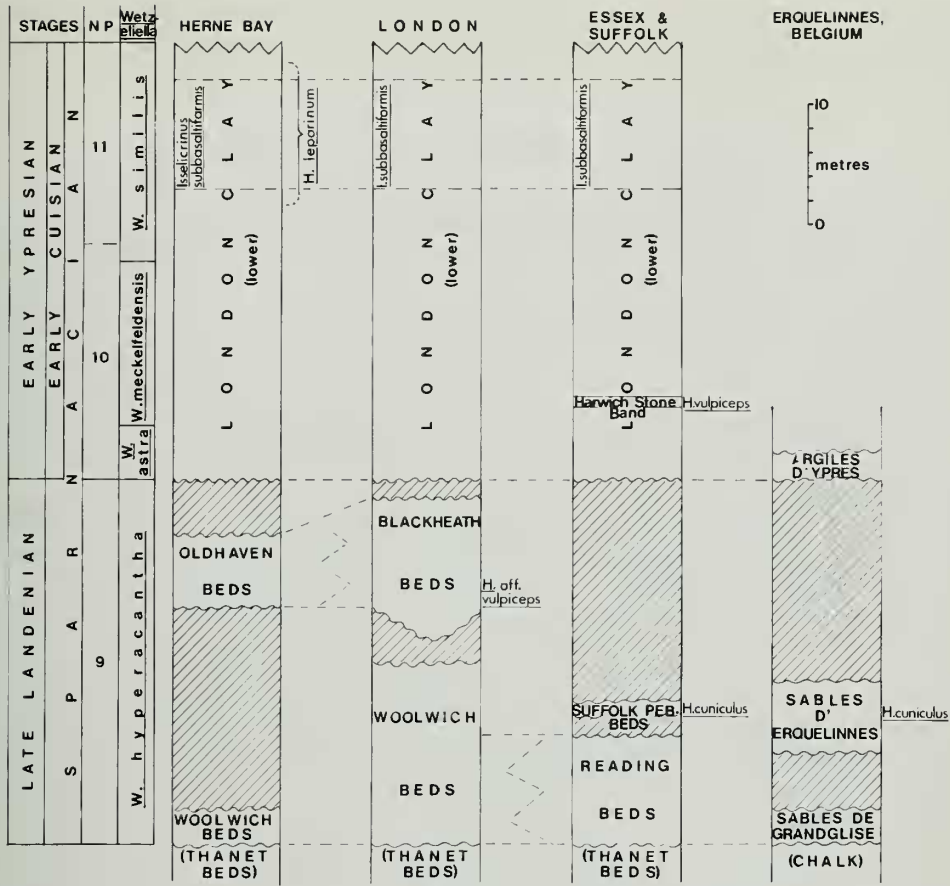


Fig. 6 Stratigraphic columns showing occurrences of English *Hyracotherium* and correlation with Belgium. The *Wetzeliella* and standard calcareous nannoplankton zones (NP) are after Costa & Downie (1976) and Costa *et al.* (1978). Oblique hatching indicates absence of deposits. The range given for *Isselicrinus subbasaltiformis* follows King (1970).

Beds localities on the common occurrence of *H. cuniculus*, and is here considered to be early Sparnacian. Recently Costa *et al.* (1978) correlated the French Sables de Cuise (type Cuisian) with the English London Clay, already correlated with the Belgian Argiles d'Ypres (type Ypresian) by Costa & Downie (1976), and the French Sparnacian strata with the English Woolwich/Reading Beds and Blackheath/Oldhaven Beds, on the basis of a succession of dinoflagellate zones. This would appear to contradict the evidence from the mammals. However, the Sables de Sinceny and Pourcy ('Upper Sparnacian' of Costa *et al.* 1978), which immediately underlie the Sables de Cuise, have been recognized above an erosion plane in the middle of the type Sparnacian in the region of Épernay (Feugueur 1963 : 288–291). The mammaliferous horizons of Mutigny and Avenay appear to lie above this level (Michaux 1964; Louis 1970 : 58–60) and could therefore both be equivalent to lower levels of the Sables de Cuise; the higher Sables à Unios et Térédines of the Épernay district (classically considered sole Cuisian of the area) would then be equivalent to only the upper part of the type Cuisian. In that case the whole of the Sparnacian of Costa *et al.* (1978), being based on the Soissonnais area, would refer only to the lower part of the type Sparnacian.

According to these correlations, the two species of the plesiadapid primate *Platychoerops*

(*P. daubrei* (Lemoine, 1880) from Pourcy, Mutigny and Avenay and *P. richardsoni* Charlesworth, 1855, from Herne Bay), considered by Gingerich (1976 : text-fig. 19) to have an ancestor-descendant relationship, are approximately contemporaneous.

Comparison with North American material

Few valid comparisons can be made with the North American species of *Hyracotherium* until they are thoroughly revised in a detailed stratigraphic context. Kitts (1956) evidently reduced the number of valid species too drastically without sufficiently good stratigraphic control (see comments by McKenna 1960 : 117–119, Delson 1971 : 355–356, and Guthrie 1967 : 42–45). A few general points can be made. The buccal flexure of the centrocrista and development of the mesostyle on upper molars had hardly begun before the late Wasatchian (e.g. Wind River and Lost Cabin faunas). Moreover, the enlargement of the P³ protoconule, heralding the pre-molar molarization of *Orohippus*, had not taken place until this time. English and continental European *Hyracotherium* species appear to have been more precocious in their evolution, as were the later more advanced European palaeotheres over their contemporaneous North American equid relatives.

As in Europe, most of the North American records of *Hyracotherium* are from the early Eocene, but two have been attributed to the Palaeocene (Morris 1968 : 1, Jepsen & Woodburne 1969). The latter record has been discredited by Gingerich (1976 : 51–53) as being in an area of downwardly younger (Wasatchian) early Eocene strata amongst generally older (Palaeocene) strata. The former record is of a small species (*H. seekinsi* Morris, 1968) from the Tepetate Formation of Baja California, Mexico, associated with barylambdid pantodonts and *Esthonyx* sp. The species is based on a few isolated upper molars and appears scarcely more primitive than typical early Wasatchian species, e.g. *H. angustidens* (Cope). Gingerich (1976 : 56–58) correlated the Clarkforkian (the stage immediately preceding the Wasatchian in North America) with the lower Sparnacian of Europe, based on the evolution of plesiadapid primates. There appear to be no records of *Hyracotherium* specifically from the Clarkforkian and so, with the possible exception of *H. seekinsi*, the early Sparnacian *H. cuniculus* is the oldest species of the genus. One of its features which appears to be primitive amongst the European species is the small size of the M₃ hypoconulid lobe. M₃s of this morphology, however, appear to occur randomly in Wasatchian populations (e.g. Savage *et al.* 1965 : text-fig. 5c). This may be another reflection of the generally slower evolution of the North American species compared with the European ones, leading to retention of primitive characters in some individuals. The slightly earlier appearance of *Hyracotherium* in Europe than in the North American Rocky Mountain region might point to an immigration from the east rather than from Central America as postulated by Sloan (1970) and Gingerich (1976 : 86–88).

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